

The Triassic Amphibian *Thoosuchus yakovlevi* and the Relationships of the Trematosauroida (Temnospondyli: Stereospondyli)

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ABSTRACT. A skull of the basal trematosauroid temnospondyl *Thoosuchus yakovlevi* from the Early Triassic of Russia is described. Characters showing phylogenetic affinities with the Trematosauroida include the presence of a postorbital-prepineal growth zone, the well-developed sensory sulci, the ventrally knife-edged cultriform process of the parasphenoid, and the posteriorly expanded parasphenoid body. A preliminary phylogenetic analysis of trematosauroid relationships confirms that *Benthosuchus* is a basal trematosaurian rather than a basal mastodonsauroid, and that *Thoosuchus* is the sister group to all other trematosauroids. Relationships within the Trematosauroida are poorly established with as yet little evidence for subdivision of the group as previously proposed. In addition, the hypothesis that the Metoposauroida is nested within the Trematosauroida is supported. However, the Trematosauridae *sensu stricto* appears to be paraphyletic. The basal stereospondyl dichotomy between the Mastodonsauroida and its relatives (the Capitosauria), and the Trematosauroida and its relatives (the Trematosauria), is supported, and now seems well established.

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The Trematosauridae is a diverse and cosmopolitan group of temnospondyl amphibians known from the Early, Middle and Late Triassic, and from all continents except South America and Antarctica. A review of the fossil record of trematosaurids can be found in Schoch & Milner (2000). Typical trematosaurids are distinctive in possessing narrow, moderately to highly elongated snouts with large palatal fangs, paired anterior palatal vacuities, an expanded postorbital-prepineal growth zone, a knife-edged cultriform process of the parasphenoid, an elongated basicranium, and a ventrally underplated exoccipital. The Trematosauridae is traditionally subdivided into two or three taxonomic groups, the highly-derived long-snouted Lonchorhynch-

inae, which make their first appearance in the earliest Triassic, and the short-snouted Trematosaurinae and Lyrocephalinae, which appear later in the Early Triassic (Säve-Söderbergh, 1935; Cosgriff & Garbutt, 1972; Hammer, 1987; Welles, 1993). Although most trematosaurids are easily recognizable as either lonchorhynchine or trematosaurine/lyrocephaline, the relationship between these subgroups is unclear because of their morphological disparity, the temporal gap, and the fact that the apparently more primitive taxa appear later in the fossil record. This has led to suggestions that the Trematosauridae may be diphyletic in origin (Bystrow & Efremov, 1940; Shishkin, 1964; Welles, 1993). Hence, this subdivision may simply

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represent a convenient morphology-based grouping.

The origin of the Trematosauridae has been linked to a number of primitive, trematosaurid-like temnospondyls from the Early Triassic of Russia, the most widely cited of which are *Benthosuchus* (Bystrow & Efremov, 1940) and *Thoosuchus* (Riabinin, 1926). These genera are usually grouped together in the higher-level taxon Benthosuchidae (Efremov, 1940), which is thus considered by some workers (Hartmann-Weinberg & Kuzmin, 1936; Efremov, 1940; Shishkin, 1964, 1980; Getmanov, 1982, 1989; Shishkin & Welman, 1994) to include the ancestors of the Trematosauridae. Cladistic support for this hypothesis was first provided by Milner (1990), in his insightful hand-drawn phylogeny of temnospondyls. In that phylogeny, a more restricted Thoosuchidae (=Thoosuchinae of Getmanov, 1982) formed the paraphyletic stem group of a clade consisting of the Trematosauridae, Laticopidae and Metoposauridae, and the Benthosuchidae (=Benthosuchinae of Getmanov, 1982) was placed in a more basal position within the phylogeny. In marked contrast, other workers (Romer, 1947; Morales & Kamphausen, 1984; Kamphausen, 1989) consider the Benthosuchidae (*sensu lato*) to be more closely related to the Mastodonsauroidea (the senior synonym of the more widely known Capitosauroida: Damiani, 2001a). Warren & Black (1985) allied the Trematosauridae with the Rhytidosteidae in a monophyletic Trematosauroida, which they considered far removed from the Benthosuchidae and "Capitosauridae". This hypothesis was adopted by Hammer (1987). None of the above hypotheses, however, were based on analyses of a data matrix.

The recent computer-based parsimony analyses of Yates & Warren (2000) and Damiani (2001a) found *Thoosuchus* to be the sister-taxon to the Trematosauridae in a monophyletic Trematosauroida, whereas *Benthosuchus* was found to be more closely related to the Mastodonsauridae. Thus *Thoosuchus* and *Benthosuchus* were found to be only distantly related within the Stereospondyli (*sensu* Yates & Warren, 2000), and their phenetic similarity as due to their relatively plesiomorphic nature. However, the relationships within the Trematosauridae were not tested in either analysis, and in the analysis of Damiani (2001a) the Mastodonsauroidea was the sister-taxon to the Trematosauroida, whereas in Yates & Warren (2000) the latter were more closely related to a clade consisting of the Metoposauroida, Plagiosauroida, Rhytidosteidae and Brachyopoida. Interestingly, the problematic *Luzocephalus* (Shishkin, 1980), which was not included in Damiani's (2001a) analysis, was the sister-taxon to the *Thoosuchus*-Trematosauridae dichotomy in Yates & Warren (2000).

In the computer-based analysis of Schoch (2000), the basal trematosauroids *Benthosuchus* and *Thoosuchus* formed successive stem-taxa to the trematosaurids, which also included *Wetlugasaurus* as the most basal stem-trematosauroid, while the Trematosauroida was found to be the sister-taxon to the Mastodonsauroidea, contra Yates & Warren (2000). This same hypothesis of relationships was proposed in the hand-crafted phylogeny of Schoch & Milner (2000), but in addition the Metoposauroida was nested deeply within the Trematosauroida; the latter consisted of two monophyletic groupings: the Trematosauridae *sensu stricto* (Trematosaurinae, Lonchorhynchinae and Tertreminae), and a large clade consisting of the Platystegidae, Lyrocephaliscidae, Almasauridae and Metoposauridae as successively more derived groups.

Finally, Steyer's (2002) computer-based analysis of trematosaurid intrarelationships found support for a monophyletic Trematosauridae consisting of the subgroups Trematosaurinae and Lonchorhynchinae, with *Watsonisuchus* (*sensu* Damiani, 2001a) and *Benthosuchus* forming successive stem-taxa to the Trematosauridae. The Metoposauroida fell well outside of the trematosaurid clade, whereas *Luzocephalus* was found to be nested within the Trematosaurinae.

It is apparent that the phylogeny of trematosaurids remains contentious, but only the analysis of Steyer (2002) has addressed the problem by means of parsimony analysis of a data matrix. Recently, we examined two superb skulls of the trematosauroid *Thoosuchus yakovlevi*, providing the stimulus for a broad cladistic analysis of trematosauroid relationships. Thus, the aims of this paper are to investigate basal trematosaurid phylogeny, determine the broad-scale relationships within the Trematosauridae (i.e. the basal branching events), and determine how the Trematosauridae is related, in the broadest sense, to other stereospondyls. We emphasize that our analysis is preliminary due to the poorly known nature of many trematosaurids; redescrptions of much of this material are currently being undertaken by Lindemann, Sengupta, Steyer, and the senior author, and will provide sorely needed data for future, more detailed cladistic studies. As a number of descriptions of the skull of *T. yakovlevi* are available in the literature (Riabinin, 1926; Hartmann-Weinberg & Kuzmin, 1936; Efremov, 1940; Getmanov, 1989), here we emphasize only characters of phylogenetic significance as a prelude to our phylogenetic analysis.

Materials and methods

The specimens of *Thoosuchus yakovlevi* used in this study, AM F98271 and WAM 96.8.1, were purchased from a commercial fossil dealer in Melbourne, Australia, by the Australian Museum and the Western Australian Museum, respectively, and subsequently made available to us for study. These specimens were bought with the knowledge of the Palaeontological Institute, Moscow, and were not amongst the temnospondyl specimens stolen from that institution (Shishkin, 1992). Little is known as regards the history of the specimens except that labels associated with both indicate that they came from the Tikhvinskoye locality (Novikov & Sennikov, 1995) on the north bank of the Volga River near the city of Rybinsk, Yaroslavl Province, Russia. This locality has yielded dozens of three-dimensionally preserved skulls of *T. yakovlevi*, most of which are housed in the Palaeontological Institute, Moscow (Getmanov, 1989). All of the known species of *Thoosuchus* (Getmanov, 1989) come from the Rybinskian Horizon of the Vetluga Series of European Russia, of late Early Triassic (Lower Olenekian) age (Ivakhnenko *et al.*, 1997).

The description below is based exclusively (unless otherwise stated) on AM F98271, an excellently preserved, distortion-free skull. However, the anteriormost region of the snout, a small section of the right palatine ramus of the pterygoid, a section of the left maxillary tooth row, and the tip of the left tabular horn are missing. In addition, the right posterolateral region of the skull roof, including most of the right tabular horn, is not preserved but has been cleverly reconstructed in plaster. AM F98271 was preserved in a fine-grained sandstone matrix. Details of the

endocranium are therefore gleaned from WAM 96.8.1, which has been acid prepared.

In our phylogenetic analysis, we follow the methodology of phylogenetic taxonomy. Thus, higher-level taxon names referred to in the text are defined phylogenetically (i.e. in terms of ancestry) and lack Linnean rank.

Institutional abbreviations used in the text are as follows: AM, Australian Museum, Sydney; BMNH, Natural History Museum, London; NM, National Museum, Bloemfontein; NMV, Museum of Victoria, Melbourne; PIN, Palaeontological Institute, Moscow; SAM, South African Museum, Cape town; UCMP, University of California Museum of Paleontology, Berkeley; WAM, Western Australian Museum, Perth.

Anatomical abbreviations used in the text are as follows: apv, anterior palatal vacuity; ch, choana; cm, *crista muscularis* of the parasphenoid; co, *crista obliqua* of the pterygoid; ect, ectopterygoid; eo, exoccipital; f, frontal; fm, foramen magnum; fs, *fossa subrostralis media*; ht, hyoid tubercle; ic, infraorbital canal; j, jugal; jc, jugal canal; l, lacrimal; lp, lamellose process of the exoccipital; mx, maxilla; n, nasal; na, naris; oc, occipital canal; p, parietal; pal, palatine; pf, parietal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pop, paroccipital process; pp, postparietal; pqf, paraquadrate foramen; prf, prefrontal; psp, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; sc, supraorbital canal; smx, septomaxilla; sq, squamosal; st, supratemporal; t, tabular; tc, temporal canal.

Description

The skull of *Thoosuchus yakovlevi* (Figs. 1, 2) is wedge-shaped in outline and somewhat narrower than in *Benthosuchus* (Bystrow & Efremov, 1940) or mastodonsauroids. The orbits are situated approximately one-third of the way back on the lateral margins of the skull; their margins are not everted or “raised”. The nostrils are oval but are clearly less elongated than those in *Benthosuchus*. A well-developed otic notch is present posteriorly, but is not as deeply incised as the otic notch of mastodonsauroids.

Ornament on the skull roof (Figs. 1A, 2A) is of the normal pattern and distribution found in most Mesozoic stereospondyls, with an additional, albeit poorly defined, area of ridge-groove ornamentation between the orbits and the pineal. This pattern is most clearly seen on the parietals. Ridge-groove ornament in this area is characteristic of trematosaurids (Säve-Söderbergh, 1937) and is held to indicate a “zone of intensive growth” (Bystrow, 1935) on the skull.

The well-developed lateral line system is represented by near-continuous grooves for the infraorbital, supraorbital, jugular and temporal canals, as well as an occipital sulcus which runs across the posterior margin of the skull deck. An anterior sulcus is also normally present (Getmanov, 1989) but not preserved in AM F98271. The absence of an occipital sulcus in a specimen illustrated by Getmanov (1989) may indicate a degree of variability in the expression of this character. An occipital sulcus is also present in other trematosaurids including *Angusaurus* (Getmanov, 1989; Novikov, 1990), *Trematosaurus* (Säve-Söderbergh, 1937), *Wantzosaurus* (Steyer, 2002) and some specimens of *Benthosuchus* (Bystrow & Efremov, 1940; Getmanov, 1986). The infraorbital sulcus forms a step-shaped rather

than Z-shaped flexure on the lacrimal bone, as in *Angusaurus*. In *Trematosaurus brauni* (Säve-Söderbergh, 1937) and derived trematosaurids, the infraorbital canal forms a smooth, sigmoidal curve. As in trematosaurids and some mastodonsaurids (Schoch & Milner, 2000; Damiani, 2001a), the supraorbital sulcus enters the lacrimal bone.

The arrangement of the dermal roofing bones is well known from the literature and only a few points will be raised here. Posterior to each nasal a small, triangular, ornamented septomaxilla is present as part of the skull roof. Ornamented septomaxillae have also been reported in various trematosaurids including *Angusaurus* (Getmanov, 1989) and *Trematosuchus* (Shishkin & Welman, 1994) but not in *Trematosaurus*. In contrast, the septomaxilla of mastodonsaurids appears to be attached to the inside of the naris (Mukherjee & Sengupta, 1998). The tabular horns of *Thoosuchus*, like those of trematosaurids, are short and triangular in shape, and contrast with those of mastodonsaurids which are elongated and (usually) rounded distally. The postorbitals resemble those of trematosaurids in being elongated, with no indication of expansion (“hooking”) along the posterolateral orbital margin as in mastodonsaurids (Damiani, 2001a). As in *Benthosuchus*, *Angusaurus* and *Trematosaurus*, the frontals are primitively (Damiani, 2001a) excluded from the orbital margins and the projection of the jugals is greater posterior to the orbits than anterior to them. In contrast, in mastodonsaurids the frontals enter the orbital margin and there is a markedly elongated preorbital projection of the jugal.

The palate (Figs. 1B, 2B) displays narrow, elongated interpterygoid vacuities and paired anterior palatal vacuities. Between the latter, a shallow, circular depression, the *fossa subrostralis media* (Shishkin & Welman, 1994), is present, but has not been illustrated previously. This character is found in trematosaurids, archegosaurids and various other temnospondyls.

The cultriform process of the parasphenoid is deep, narrow and “knife-edged” ventrally, and the corpus of the parasphenoid is elongated. The latter is a derived character (e.g., Damiani, 2001a) and also occurs in *Angusaurus*, trematosaurids, derived mastodonsaurids and most brachyopoids. Also conspicuous is the posterior spreading of the parasphenoid to partially cover the subotic processes of the exoccipitals. In trematosaurids, this spreading is complete so that the exoccipitals are completely hidden ventrally (Warren & Black, 1985). Weakly developed, posteromedially oriented crests, the *crista musculari* (Bystrow & Efremov, 1940), are present on the base of the corpus of the parasphenoid. These are mainly exposed ventrally and to a lesser extent on the side walls (i.e. subotic process) of the exoccipital, as in lydekkerinids (Shishkin *et al.*, 1996). As in *Benthosuchus*, *Angusaurus*, *Trematosaurus*, and some basal mastodonsaurids (Damiani, 2001a), the vomers form long, posteriorly directed processes which underplate the anterior portion of the cultriform process of the parasphenoid. The long ectopterygoids are broadly exposed in the margin of the interpterygoid vacuities, as in *Trematosaurus*, *Angusaurus*, and trematosaurids but not *Benthosuchus* or mastodonsaurids (Damiani, 2001a).

The maxillary teeth are simple, conical, rounded at their bases, and increase gradually in size from posterior to anterior. Most of these remain embedded in matrix but there were at least 70 teeth on the left maxilla. A continuous

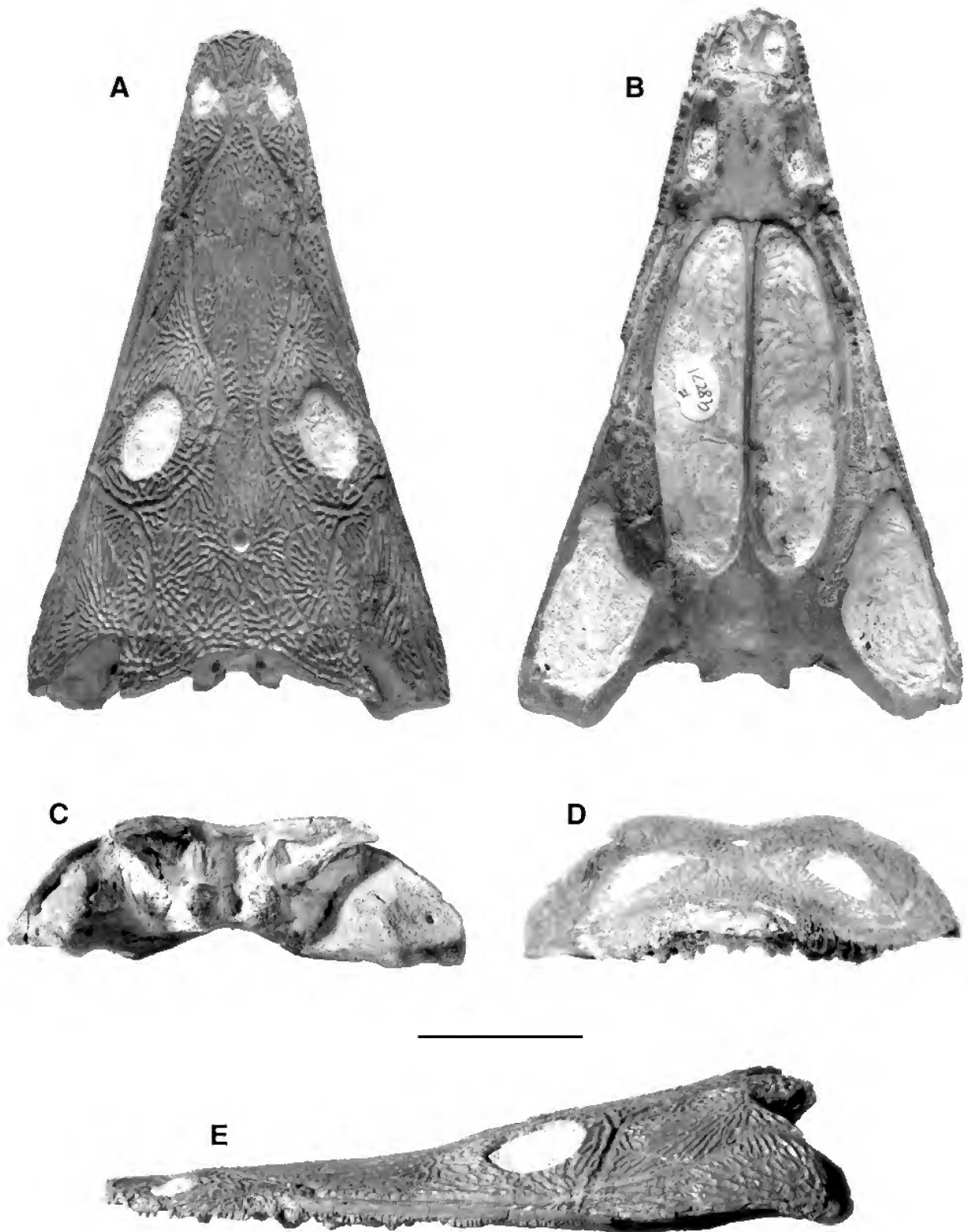


Fig. 1. *Thoosuchus yakovlevi* (AM F98271), a basal trematosauroid temnospondyl from the Early Triassic of Russia. Photographs of the skull in (A), dorsal; (B), ventral; (C), occipital; (D), anterior and (E), lateral views. Scale bar equals 30 mm.

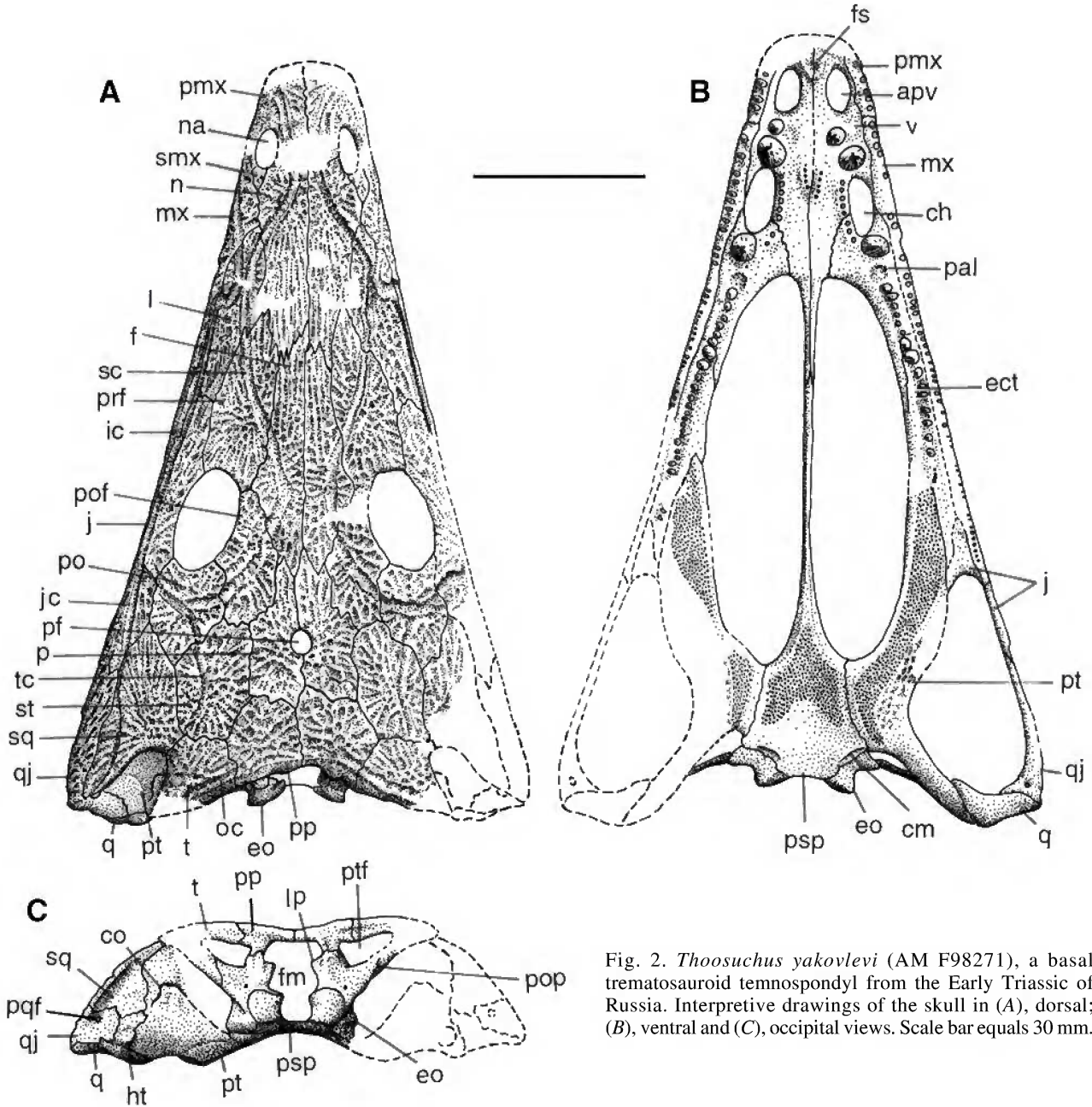


Fig. 2. *Thoosuchus yakovlevi* (AM F98271), a basal trematosauroid temnospondyl from the Early Triassic of Russia. Interpretive drawings of the skull in (A), dorsal; (B), ventral and (C), occipital views. Scale bar equals 30 mm.

tooth row and tusks are found on each of the vomers, palatines and ectopterygoids. The ectopterygoid tusks are poorly developed in AM F98271 and a small, presumably immature individual of this species (PIN 3200/279) lacks them altogether (Warren pers. comm.), suggesting late ontogenetic development of this character. Curiously, in the mastodonsaurids *Watsonisuchus aliciae* (Warren & Hutchinson, 1988; Warren & Schroeder, 1995) and *Wellesaurus peabodyi* (Welles & Cosgriff, 1965; RJD pers. obs.), ectopterygoid tusks are present in pre-adult but lost in adult individuals. A weakly developed, acutely V-shaped transvomerine tooth row is present well posterior to the anterior palatal vacuities. Conspicuous areas of denticles are present on the corpus of the parasphenoid and base of the cultriform process, and on the corpus and palatal ramus of the pterygoids. Small, faint patches of ornament are also present on the base of the corpus of the parasphenoid and on the pterygoids bordering the subtemporal vacuities.

In occipital view (Figs. 1C, 2C), the weakly developed *crista obliqua* of the pterygoid (Bystrow & Efremov, 1940) forms a very short, narrow lamina separated from the ascending ramus by a narrow slit. This differs from that of *Benthosuchus* (Getmanov, 1989) and Mastodonsaurids in which the lamina is tall and crest-like and borders a distinct channel. The occipital margin of the squamosal bears a short flange along most of its length which probably represents a reduced *crista falciformis* (Bystrow & Efremov, 1940). There is no palatoquadrate fissure in AM F98271, but one was illustrated in a specimen of *T. yakovlevi* by Getmanov (1989). However, the presence of this fissure may hinge on the degree of ossification and/or ontogeny. A palatoquadrate fissure is absent in *Angusaurus* (Getmanov, 1989), *Trematosaurus* (Watson, 1919), all other trematosaurids, and mastodonsaurids.

The ascending ramus of the pterygoid, visible in WAM 96.8.1 only, is nearly straight in dorsal view with only the

slightest hint of being recurved anteriorly. A moderate vertical thickening of its anterior margin represents the crista praeotica lamina ascendens (Getmanov, 1989), a structure thought to be present in all stereospondyls except *Lapillopsis* (Yates, 1999) and brachyopids (Damiani & Warren, 1996).

The ridges found on the ventral surface of the tabular horns in *Benthosuchus* (Bystrow & Efremov, 1940) and mastodontosaurids are not visible in *Thoosuchus* because the tips of both tabular horns are missing. As in all mastodontosaurids and *Trematosaurus* (Watson, 1919), the paroccipital processes bear a longitudinal *crista muscularis* along their posteroventral faces. A hyoid tubercle or quadrate “boss” is present on the occipital face of the quadrate near its suture with the pterygoid. This structure is present in *Benthosuchus* and mastodontosaurids but appears to be absent in trematosaurids.

Phylogenetic analysis

Methods. The phylogenetic analysis presented here is intended to cover the diversity of putative stem-group trematosaurids, trematosaurines, and lonchorhynchines. Thus only select, well-known trematosaurid taxa have been used. The remaining terminals consist of a selection of genera and higher-level taxa that have been allied by one or more authors with some or all trematosaurids, as discussed in the Introduction. The 18 ingroup taxa, and the principal references used in coding the matrix, are as follows: the putative basal trematosaurids *Benthosuchus* (Bystrow & Efremov, 1940; Getmanov, 1989; RJD pers. obs. BMNH R7992), *Thoosuchus* (this paper) and *Angusaurus* (Getmanov, 1989), the trematosaurids *Trematosaurus* (Watson, 1919; Säve-Söderbergh, 1937; Schoch & Milner, 2000; RJD pers. obs. NMV P175723), *Tertrema* (Wiman, 1914; Säve-Söderbergh, 1936), *Lyrocephaliscus* (Säve-Söderbergh, 1936; Mazin & Janvier, 1983), *Platystega* (Säve-Söderbergh, 1936), *Microposaurus* (Haughton, 1925; RJD pers. obs. SAM-PK-6556), *Aphaneramma* (Säve-Söderbergh, 1935, 1936) and *Cosgriffius* (Welles, 1993), the mastodontosaurids *Watsonisuchus* (Warren, 1980; Damiani, 2001a; RJD pers. obs. NM QR3043), *Wetlugasaurus* (Sennikov, 1981; Schoch & Milner, 2000) and *Parotosuchus* (Damiani, 2001b), the almasaurid *Almasaurus* (Dutuit, 1976), the putative lydekkerinid *Luzocephalus* (Shishkin, 1980; Bjerring, 1999), and the higher-level taxa Metoposauridae, Lydekkerinidae and Rhytidosteidae, which were coded according to their bauplans. The data matrix (Table 1) was coded according to the adult (or presumed adult) condition for each character. A comprehensive list of references for the above taxa can be found in Schoch & Milner (2000). We have not included the Brachyopoidea in our analysis because their supposed closer relationship to the Mesozoic Stereospondyli than to Palaeozoic short-faced taxa is far from certain (e.g., Foreman, 1990; Milner, 1990; Damiani & Kitching, 2003; but see Yates & Warren, 2000 for a contrasting view). The outgroups used to determine character polarity are the Archegosauridae (Gubin, 1991, 1997) and the Rhinesuchidae (Watson, 1962). These higher-level taxa are widely considered to be successive outgroups to most or all of the Mesozoic stereospondyls (Milner, 1990; Schoch & Milner, 2000; Yates & Warren, 2000).

The analysis was based on 40 cranial characters (Table 2). Characters 5, 8, 10, 13, 16, 18, 22, 27, 29, 30 and 37 are multistate characters but only characters 5, 8, 13, 18 and 27 form clear transformation series and were thus ordered. All characters remained unweighted. Taxa having multiple states were treated as polymorphic. The data were analysed using the Heuristic search of PAUP 3.1.1 (Swofford, 1993) with the following settings: the tree-bisection-reconnection branch-swapping algorithm was used and trees obtained via the simple stepwise-addition sequence, zero-length branches were collapsed to yield polytomies, and all the shortest trees were kept. Characters were optimized under the Deltran algorithm.

Results and discussion. The analysis produced ten most parsimonious trees (MPTs) each of 109 steps, a consistency index of 0.523 and a retention index of 0.745. The composition of the Trematosauroidae is identical in these trees, varying only in the topology of the clade that includes *Aphaneramma*, *Cosgriffius*, *Platystega* and *Tertrema*. Figure 3A represents one of the ten MPTs chosen as our phylogenetic hypothesis on the basis of a *posteriori* assessment of character distribution. Nodes A through F on this cladogram are discussed below. A strict consensus of the ten trees, along with the decay index for each node, is shown in Figure 3B.

The broad-scale results of our phylogeny are in most ways consistent with recent phylogenetic hypotheses of stereospondyl relationships (Schoch & Milner, 2000; Yates & Warren, 2000). However, it differs markedly in the position of the Rhytidosteidae, which in those analyses is nested deeply within the Stereospondyli in a more derived position than the Capitosauria and Trematosauria. Here, the Rhytidosteidae is the sister-group to *Luzocephalus* (node B), as in the hypothesis of Milner (1990). This relationship is supported by two unambiguous synapomorphies: the absence of muscular pockets (*crista musculari*) on the ventral surface of the corpus of the parasphenoid (character 22, state 0), representing an apomorphic reversal, and the presence of a palatoquadrate fissure (character 33, state 1). The clade [Rhytidosteidae + *Luzocephalus*] is the sister-group to the Lydekkerinidae, a hypothesis broadly similar to that of Milner (1990) and Schoch & Milner (2000), but at odds with that of Yates & Warren (2000) who allied the Lydekkerinidae with the Mastodontosauroidae. This clade (node A) is supported by two unambiguous synapomorphies, the foreshortened snout (character 4, state 0) and the absence of a *crista falciformis* of the squamosal (character 10, state 0), and one ambiguous synapomorphy, the presence of a single anterior palatal vacuity (character 16, state 2), all representing apomorphic reversals. However, this clade is not robust and requires only one additional step to shift the Lydekkerinidae to various other basal positions within the Stereospondyli. Clearly, the position of the Lydekkerinidae within the Stereospondyli remains contentious. Similarly contentious is the affinities of *Luzocephalus*, which has elsewhere been allied with lydekkerinids (Shishkin *et al.*, 1996; Schoch & Milner, 2000) or trematosaurids (Yates & Warren, 2000; Steyer, 2002).

The remaining clade of “higher” stereospondyls (node C) consists of a sister-group relationship between the Capitosauria (node D) and the Trematosauria (node E), and

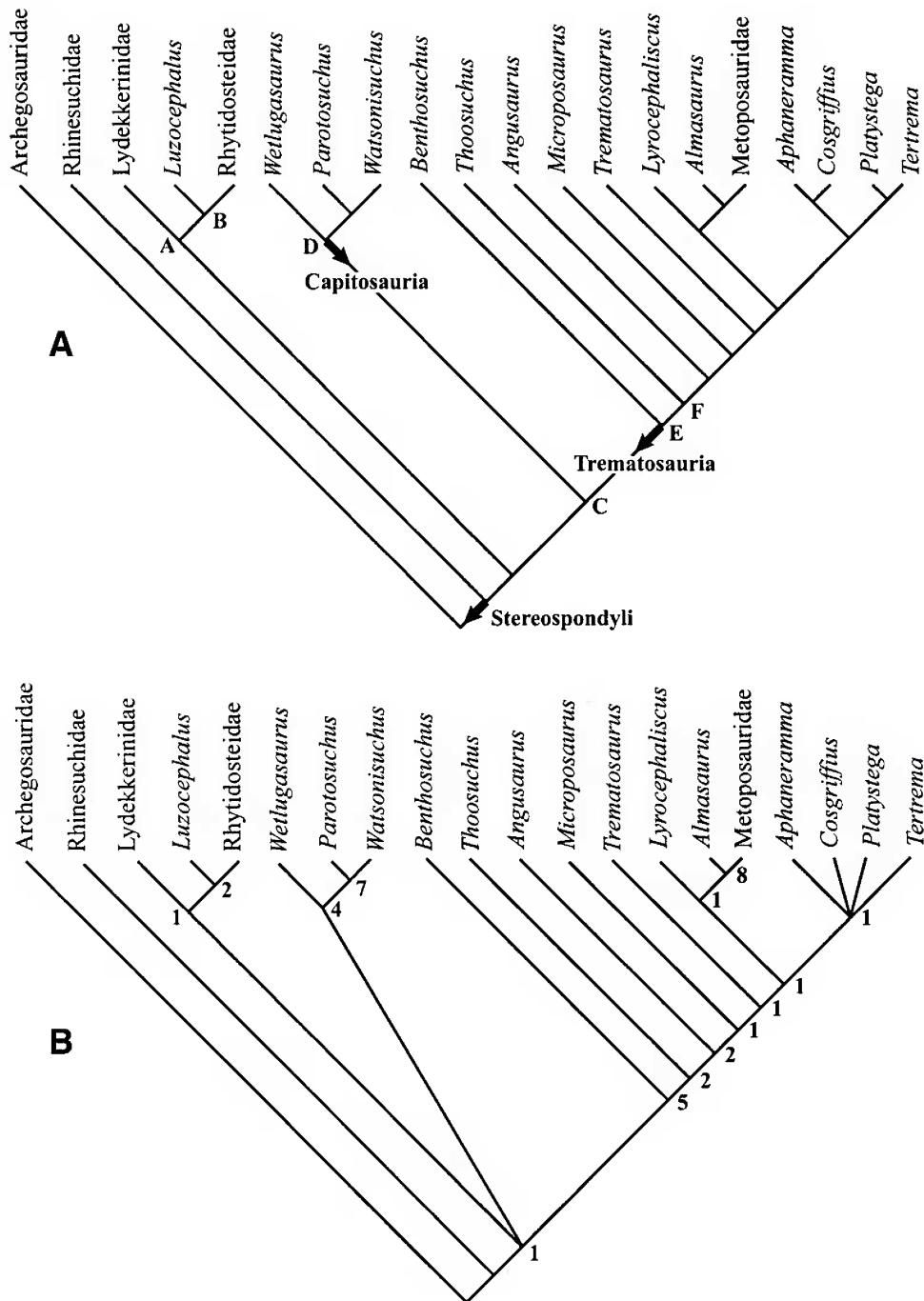


Fig. 3. Phylogeny of trematosauroid temnospondyls and related taxa resulting from a PAUP analysis of the data matrix presented in Table 1. (A), preferred phylogeny representing one of the ten most parsimonious trees (MPTs), showing the Capitosauria and Trematosauria (denoted by short arrows) as defined by Yates & Warren (2000). Nodes A–F discussed in the text. (B), strict consensus of ten MPTs, showing decay index for each clade.

is supported by one ambiguous synapomorphy, the step-shaped lacrimal flexure (character 13, state 1), and one unambiguous synapomorphy, the presence of teeth on the posterior coronoid only (character 37, state 1). A similar basal stereospondyl dichotomy between the Mastodontosauridae (or Mastodontosauroida in more inclusive analyses) and the Trematosauroida was found by Schoch (2000), Schoch & Milner (2000), Yates & Warren (2000) and Damiani (2001a). Yates & Warren (2000) erected the terms Capitosauria and Trematosauria to refer to the Mastodontosauroida and its stem-group, and the Trematosauroida

and its stem-group, respectively, and provided formal phylogenetic definitions for these taxa. Yates & Warren (2000) defined the Trematosauria as all stereospondyls sharing a more recent common ancestor with *Trematosaurus* than with *Parotosuchus*, and the Capitosauria as all stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Siderops*. Under the latter definition, however, the composition of the Capitosauria can alter drastically depending upon the phylogenetic position of *Siderops* (Brachyopoidea) within temnospondyl phylogeny. If, as various authors have argued, the

Brachyopoidea do not form part of the Stereospondyli, then the Capitosauria could potentially include most of the Stereospondyli. Thus we advocate a slightly modified definition of the Capitosauria: All stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Trematosaurus*. This definition remains relatively insensitive to large-scale shifts in the position of the Brachyopoidea while maintaining the integrity of the basal dichotomy between mastodontosaurids and trematosauroids. Although Schoch & Milner (2000) used the term Capitosauria to refer to the large clade formed by the "Capitosauroida" and Trematosauroida, they did not define it phylogenetically.

In most previous hypotheses of mastodontosaurid relationships, *Wetlugasaurus* has been considered either a basal mastodontosaurid or a sister-group to them (e.g., Ochev, 1966; Ingavat & Janvier, 1981; Kamphausen, 1989; Milner, 1990; Maryanska & Shishkin, 1996; Damiani, 2001a). However, in the recent phylogenetic analyses of Schoch (2000) and Schoch & Milner (2000), *Wetlugasaurus* was considered the most basal stem-trematosauroid, with *Benthosuchus* and *Thoosuchus* forming successively more derived outgroups to the remaining trematosauroids. The synapomorphies used to support this arrangement are as follows (our numbering): (1) presence of a V-shaped transvomerine tooth row; (2) processus parasphenoidales of the vomers which conceal the cultriform process anteriorly; (3) narrow, elongated frontals, postfrontals and postorbitals; (4) small orbits located anterolaterally on the skull roof; (5) nostrils located medially on the snout which is elongated anterior to them. Of these, character (3) pertains only to trematosaurids in which a postorbital-prepineal growth zone has developed, a condition not met in *Wetlugasaurus*; character (4) does not pertain to *Wetlugasaurus* because its orbits are large and located within the posterior half of the skull roof; and character (5) does not

pertain to *Wetlugasaurus* because its nostrils are located near the skull margins and the snout is not elongated anterior to them. Thus, the position of *Wetlugasaurus* in their analysis appears to hinge largely on characters (1) and (2) above. In contrast, our analysis supports the traditional hypothesis of inclusion of *Wetlugasaurus* in the Mastodontosauridae (node D). This clade requires four additional steps in order to make *Wetlugasaurus* the most basal stem-trematosauroid, and its monophyly is supported by one ambiguous synapomorphy, the presence of a single anterior palatal vacuity (character 16, state 2), representing an apomorphic reversal, and six unambiguous synapomorphies, the well-developed *crista falciformis* of the squamosal (character 10, state 2), the Z-shaped lacrimal flexure (character 13, state 2), the transversely expanded *crista musculari* of the parasphenoid (character 22, state 2), the strongly anteroposteriorly compressed tooth bases (character 28, state 1), the tall, crest-like oblique ridge of the pterygoid (character 34, state 2), and the well-developed hamate process of the prearticular (character 38, state 1). Nevertheless, we concede that the presence of characters (1) and (2) above, along with exclusion of the frontal from the orbital margin (a symplesiomorphy), are persuasive characters tying *Wetlugasaurus* to trematosauroids. Full resolution of this problem must await the discovery of additional fossils in the critical period prior to the initial radiation of the Mesozoic stereospondyls, an event which probably occurred in the latest Permian (Yates & Warren, 2000; Warren *et al.*, 2000; Damiani, 2001a).

The hypothesis that the Trematosauridae may be diphyletic in origin (Shishkin, 1964; Welles, 1993) is not supported by our analysis, which recognizes only one monophyletic group (node E). *Benthosuchus*, *Thoosuchus* and *Angusaurus* form a series of stem-taxa of the remaining trematosauroids, as also found by Schoch (2000) and Schoch & Milner (2000). This clade (node E) is strongly

Table 1. Data matrix and character distribution. Character states are denoted by the following symbols: 0 = primitive; 1, 2, 3 = derived; ? = state unknown due to inadequate preservation; dash (-) = character inapplicable; P = polymorphic (states 0 and 1 present).

Characters	00000	00001	11111	11112	22222	22223	33333	33334
Taxa	12345	67890	12345	67890	12345	67890	12345	67890
<i>Almasaurus</i>	01100	00011	11010	31210	00110	12022	1100?	0201?
<i>Angusaurus</i>	11111	00010	01111	31200	10101	10012	10010	01010
<i>Aphaneramma</i>	11112	00010	01011	31100	10111	?2010	10110	0001?
<i>Benthosuchus</i>	10011	00111	01111	31100	11000	00012	11010	01000
<i>Cosgriffius</i>	11112	100??	?10-?	00??0	1????	??0?0	10???	?????
<i>Luzocephalus</i>	00000	00110	00000	21100	00000	00011	11110	1????
Lydekkerinidae	00000	00110	00100	20100	01000	00011	11010	10000
<i>Lyrocephaliscus</i>	11100	00010	01011	31200	10101	?1011	10120	0????
Metoposauridae	01100	00012	111-0	30211	01110	12021	11001	?0011
<i>Microposaurus</i>	01101	00010	010??	3?200	10101	?0000	10???	0????
<i>Parotosuchus</i>	00010	01212	00200	20100	02000	00121	11020	01101
<i>Platystega</i>	01111	00010	0????	30200	10111	?1010	10???	?????
Rhytidosteidae	01000	10010	000-0	20-00	00000	00000	10100	00001
<i>Tertrema</i>	11111	00010	01010	30200	10111	?00?0	00???	?????
<i>Thoosuchus</i>	11111	00011	01111	31200	11100	00012	10010	01010
<i>Trematosaurus</i>	11101	00010	01011	31200	10111	?1010	10110	01010
<i>Watsonisuchus</i>	00010	01212	00200	20100	02000	00121	11020	01101
<i>Wetlugasaurus</i>	00010	00112	00200	21100	02000	00112	11020	01100
Archeosauridae	P0011	0000P	00000	30000	01000	0000P	01010	00000
Rhinesuchidae	00010	00101	00000	10P00	01000	00001	01010	00010

Table 2. Characters and character states.

Skull Roof	
1	Skull outline in dorsal view: broad, rounded (0); narrow, wedge-shaped (1).
2	Position of orbits: medially displaced, approximately in-line with nostrils (0); laterally displaced, close to margin of skull (1).
3	Postorbital-prepineal growth zone: absent (0); present (1). In the derived state the dermal sculpturing between the orbits and the pineal includes elongated ridges and grooves forming a “zone of intensive growth” (Bystrow, 1935); that is, where strong allometric growth has occurred.
4	Length of snout (i.e. preorbital portion of skull): less than 50% of total skull length (0); greater than 50% of total skull length (1). This character pertains to adult individuals only, as the shape of the skull in juvenile temnospondyls can differ significantly from that of adults (Boy & Sues, 2000).
5	Prenarial snout length: less than internarial distance (0); equals or exceeds internarial distance (1); greater than three times internarial distance (2).
6	Lacrimal: present (0); absent (1).
7	Frontal: excluded from medial margin of orbit by prefrontal-postfrontal suture (0); enters medial margin of orbit (1).
8	Postorbital: unexpanded anterolaterally (0); moderately expanded anterolaterally (1); strongly expanded anterolaterally (2).
9	Supratemporal: enters margin of otic notch (0); excluded from margin of otic notch by squamosal-tabular suture (1).
10	<i>Crista falciformis</i> of squamosal: absent (0); weakly developed, partially constricting otic notch posteriorly (1); well developed, strongly constricting otic notch posteriorly (2).
11	Well defined gutter surrounding otic notch: absent (0); present (1).
12	Lateral line sensory sulci: weakly impressed, discontinuous (0); well impressed, continuous (1).
13	Lacrimal flexure of the infraorbital sensory sulcus: absent (0); step-shaped (1); Z-shaped (2).
14	Supraorbital sensory sulcus: excluded from lacrimal (0); enters lacrimal (1).
15	Occipital sensory sulcus: absent (0); present (1).
Palate	
16	Anterior palatal “vacuity”: absent (0); forming shallow fossa (1); single vacuity (2); paired or incipiently paired (i.e. bilobed) vacuities/foramina (3).
17	<i>Processus parasphenoidales</i> of the vomers: separated by median exposure of cultriform process of parasphenoid (0); meet in midline to conceal cultriform process anteriorly (1).
18	Contribution of palatine and ectopterygoid to margin of interpterygoid vacuity: both excluded by pterygoid-vomer contact (0); palatine only included (1); both palatine and ectopterygoid included (2). This character reflects a progressive retreat of the pterygoid from the lateral margins of the interpterygoid vacuities, and is therefore ordered.
19	Posteromedial expansion of ectopterygoid: absent (0); present, forms significant part of strut separating interpterygoid vacuity from subtemporal vacuity (1).
20	Distinct depression or foramen at anterior tip of cultriform process of the parasphenoid: absent (0); present (1).
21	Ventral surface of cultriform process of parasphenoid: simple, flattened bar (0); with midline, “knife-edged” keel (1).
22	Muscular pockets (<i>crista musculari</i>) on ventral surface of corpus of parasphenoid: absent (0); present, convex and widely spaced (1); present, transversely expanded so as to approach or merge in the midline (2).
23	Length of pterygoid-parasphenoid (basicranial) suture: shorter than width of parasphenoid body (0); longer than width of parasphenoid body (1).
24	Quadrate ramus of the pterygoid: long, posteriorly directed (0); short, posterolaterally or laterally directed (1).
25	Exoccipital: fully exposed ventrally (0); underplated by posterior extension of parasphenoid (1).
26	Ventral exoccipital-ptyerygoid suture: absent (0); present (1).
27	Position of exoccipital condyles relative to quadrate condyles: anterior to condyles (0); level or slightly posterior to condyles (1); well posterior to condyles (2).
Palatal Dentition	
28	Marginal dentition: circular to sub-circular at base (0); strongly anteroposteriorly compressed at base (1).
29	Palatal shagreen (denticles): extensive field throughout palate (0); localized patches (1); absent (2).
30	Tooth row on vomers posterior to anterior palatal vacuity: absent (0); transverse or arcuate (1); V-shaped or paired parallel rows (2).
31	Tooth row medial to choana: absent (0); present (1).
32	Ectopterygoid tusks: present (0); absent (1). This character pertains to adult individuals only, as ectopterygoid tusks are present in juvenile but not adult individuals of some species (e.g., “ <i>Parotosuchus aliciae</i> ”, <i>Wellesaurus peabodyi</i>) (Damiani 2001a).
Occiput	
33	Palatoquadrate fissure between cheek and palate: absent (0); present (1).
34	<i>Crista obliqua</i> on quadrate ramus of pterygoid: absent (0); low, rounded (1); tall, crest-like (2).
35	Post-temporal fenestrae: large, triangular (0); small, circular (1).
36	Cheek contour in occipital view: curved (0); straight (1).
Mandible	
37	Coronoid teeth: absent from all coronoids (0); present on posterior coronoid only (1); present on two or all three coronoids (2).
38	Hamate process of the prearticular: absent or rudimentary (0); large, well developed (1).
39	Length of posterior meckelian foramen: less than (or equal to) 50% of length of adductor fossa (0); greater than 50% of length of adductor fossa (1).
40	Post-symphyseal tooth row: absent (0); present (1).

supported, requiring five additional steps to break, and is diagnosed by two ambiguous synapomorphies, the *processus parasphenoidales* of the vomers which conceal the cultriform process anteriorly (character 17, state 1) and V-shaped or paired parallel transvomerine teeth (character 30, state 2), and six unambiguous synapomorphies, the narrow, wedge-shaped skull (character 1, state 1), an elongated prenarial region (character 5, state 1), well impressed, continuous sensory sulci (character 12, state 1), the supraorbital sulcus entering the lacrimal (character 14, state 1), the presence of an occipital sulcus (character 15, state 1), and a knife-edged cultriform process (character 21, state 1).

We find little support for the hypothesis that *Benthosuchus* is the most basal mastodontosaurid (Yates & Warren, 2000; Damiani, 2001a), and feel that some of the synapomorphies used to support that hypothesis are unconvincing. These include, in Yates & Warren's (2000) analysis, the presence of a ventrally open supraglenoid foramen, which does not in fact occur in mastodontosaurids (Warren & Snell, 1991) and which is known to vary with ontogeny in some taxa (Schoch, 1999), and the absence of shagreen on the coronoid series, which also occurs in trematosaurids. In Damiani's (2001a) analysis, three of the six unambiguous synapomorphies used to support the same relationship are incorrectly coded for *Benthosuchus*; these are the presence of a step-shaped lacrimal flexure, strongly anteroposteriorly compressed tooth bases, and a tall, crest-like oblique ridge of the pterygoid. We are therefore inclined to regard *Benthosuchus* as a stem-trematosauroid, as indicated by our phylogeny.

Relationships within the Trematosauroidae are poorly established, with *Microposaurus* and *Trematosaurus* forming successive stem-taxa to a clade consisting of a sister-group relationship between *Lyrocephaliscus* plus the Metoposauroidae (sensu Yates & Warren, 2000: Metoposauridae + *Almasaurus*), and a clade consisting of *Aphaneramma* and *Cosgriffius* (lonchorhynchines), *Platystega* and *Tertrema*. Thus, our phylogeny supports that of Milner (1990) and Schoch & Milner (2000), but not that of Yates & Warren (2000) or Steyer (2002), in having the Metoposauroidae nested within the trematosauroids. As a consequence, the Trematosauridae, as usually conceived, appears to be paraphyletic according to our analysis. Furthermore, the monophyly of the traditional, more restricted Trematosauridae, as conceived by earlier workers (e.g., Säve-Söderbergh, 1935; Hammer, 1987) and supported by the analyses of Schoch & Milner (2000) and Steyer (2002), could also not be supported. Thus, we see little evidence for the long-held basic subdivision of the trematosauroids into long-snouted lonchorhynchines and short-snouted trematosaurines, or of a finer subdivision into the categories of Hellrung (1987) or Schoch & Milner

(2000). Note that in our analysis most of the clades within the Trematosauroidae are tenuous and require only one additional step to break, but no tree could be obtained which showed a monophyletic Trematosauridae. We conclude that relationships within the Trematosauroidae are poorly established, and that the Trematosauridae, as traditionally conceived, is not a clade. Resolution of these problems must await redescriptions of poorly known taxa and/or additional data.

A number of authors have used the name Trematosauroidae for the clade that includes *Benthosuchus* and which would coincide with node E in our analysis (Getmanov, 1989; Schoch & Milner, 2000). However, Yates & Warren (2000) defined the Trematosauroidae as the last common ancestor of *Thoosuchus* and *Trematosaurus* and all its descendants, corresponding to node F on our phylogeny. Thus *Benthosuchus* is excluded from the Trematosauroidae, but not from the Trematosauria (sensu Yates & Warren, 2000). This definition is favourable because, although we disagree with the hypothesis that *Benthosuchus* is closer to mastodontosaurids, it remains insensitive to potential changes in the position of *Benthosuchus*.

Phylogenetic conclusions

Despite a number of recent phylogenetic analyses of stereospondyl relationships (Warren & Black, 1985; Milner, 1990; Schoch & Milner, 2000; Yates & Warren, 2000; Damiani, 2001a), it is apparent that much additional work remains before a consensus of relationships is reached. This concerns not only the broader relationships within the Stereospondyli, but also, as highlighted in our analysis of the Trematosauroidae, the relationships within particular groups.

The Trematosauroidae appears to be a well-defined group of stereospondyls within which are nested the Metoposauroidae. Consequently, the Trematosauridae, as traditionally perceived, appears to be paraphyletic. *Thoosuchus* is the most basal member of the Trematosauroidae as defined by Yates & Warren (2000), with *Benthosuchus* basal to them. Relationships within the Trematosauroidae are poorly established in our analysis, with little evidence for subdivision into lonchorhynchines and trematosaurines, or other proposed subgroups. The poor state of knowledge of many trematosaurids precludes a more detailed analysis and contributes to the low support (as indicated by decay indices) for many of the clades in our analysis. The Trematosauroidae and its relatives (the Trematosauria) share a common ancestry with the Mastodontosauroidae and its relatives (the Capitosauria), a basal stereospondyl dichotomy which now seems well established.

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